

REVIEW OF PLEISTOCENE DARKLING GROUND BEETLES OF THE
CALIFORNIA ASPHALT DEPOSITS (COLEOPTERA:
TENEBRIONIDAE, ZOPHERIDAE)

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Darkling ground beetles (Tenebrionidae) are the most abundant insects preserved in the California asphalt deposits, and have been found at Rancho La Brea, Carpinteria, McKittrick and Maricopa. A total of 33 species and subspecies have been recognized by various workers, including several which were regarded as extinct taxa. This paper reviews published reports for Rancho La Brea and McKittrick and presents new records for Carpinteria. The fossil faunas are discussed in terms of the present California tenebrionid fauna and its distribution.

The first tenebrionids recorded from the California asphalt deposits were from excavations at Rosemary, near Los Angeles. This site is now known as Rancho La Brea. These specimens were described by Grinnell (1908), who designated 3 new species of *Eleodes* from the material.

Grinnell's specimens were later examined by Blaisdell (1909:505-508) who believed they were synonymous with extant species. Essig (1931:1-11) listed several additional tenebrionids and zopherids from the La Brea deposits. After a preliminary paper (1944) in which the lists of Essig and Grinnell were repeated, Pierce (1954a, b, c) catalogued the tenebrionid faunas of La Brea and McKittrick, describing 4 new species and 8 new subspecies. Pierce did not finish his work, never publishing on *Eleodes*, and no one has worked with the material since. The Pierce types were catalogued by Sphon (1973).

Like other arthropods preserved in the asphalt deposits, tenebrionid fossils consist almost entirely of disarticulated body parts. Tenebrionid fragments useful in recognizing taxa are: 1) the head capsule; 2) the prothorax; and 3) the combined pterothorax (including elytra) and anterior three abdominal sternites. Any one of these items is usually adequate for determination to genus or species group. More precise identification, however, is most reliably made by comparing details of surface sculpturing, which, as noted by Blaisdell (1909), are often obscured or modified, even in well-

cleaned specimens. Furthermore, much of the material from the La Brea deposits appears badly abraded, probably by water transport from adjacent hills. Prominences such as the elytral humeri, the epipleural ridges and the prosternal process are rounded or sometimes obliterated in such specimens, and cuticular sculpturing and appearance are drastically altered. Some of the material studied by Grinnell and Essig was incorrectly identified because of this problem.

Pierce felt that fragments he could not associate with known species should be described as new taxa so that they could be considered "identified." Most are obviously very similar to extant species which occur in southern California today, and were described by Pierce as new subspecies. As indicated by Miller and Peck (1979), infraspecific names are inappropriate, since the fossils do not represent geographic races and there is no morphological basis upon which to found chronospecies. Consequently, these names are placed in synonymy below.

We have re-examined the material described by Grinnell, Essig and Pierce in order to provide the following lists. We have not examined the large number of unstudied tenebrionids from the recent re-excavation at La Brea Pit 91. In addition, unstudied *Eleodes* are available from the McKittrick and Maricopa asphalts.

Rancho La Brea

The Rancho La Brea asphalt deposits in Los Angeles are well known for vertebrate fossils, and have a complex history of excavation. Specimens unearthed during the early (1905–1912) excavations by the University of California are deposited at the University of California Museum of Paleontology in Berkeley. This material forms the basis of the species lists of Grinnell and Essig. The most extensive excavations were undertaken by the Los Angeles County Museum from 1913 to 1915, and included Pits 4, 9, 28 and 81, which produced many of the fossils studied by Pierce. Pits A, B, and C were excavated in 1929, and Pierce's "Bliss 29" material was collected from these sites. Pierce's "Pit(?)" or "Pit X" refers to mixed material lacking data (Pierce, 1954a), and may not be fossil. Further details of excavation are provided by Miller and Peck (1979). The following list includes the species known to be represented in the La Brea material, with synonyms listed where appropriate.

TENEBRIONIDAE

Apsena laticornis Casey [Essig, 1931; Pierce, 1954b].

Apsena labreae Pierce, 1954b. NEW SYNONYMY.

Apsena pubescens (LeConte) [Pierce, 1954b].

Apsena rufipes (Eschscholtz) [Pierce, 1954b].

- Coniontis abdominalis* LeConte [Grinnell, 1908; Pierce, 1954c].
Coniontis abdominalis caseyi Pierce, 1954c. NEW SYNONYMY.
Coniontis abdominalis fragmans Pierce, 1954c. NEW SYNONYMY.
Coniontis abdominalis labreae Pierce, 1954c. NEW SYNONYMY.
Coniontis blissi Pierce, 1954c. NEW SYNONYMY.
Coniontis pectoralis interrupta Pierce, 1954c. NEW SYNONYMY.
Coniontis pectoralis paraelliptica Pierce, 1954c. NEW SYNONYMY.
Coniontis tristis alpha Pierce, 1954c. NEW SYNONYMY.
Coniontis tristis asphalti Pierce, 1954c. NEW SYNONYMY.
Coniontis tristis latigula Pierce, 1954c. NEW SYNONYMY.
Coniontis elliptica Casey [Grinnell, 1908; Pierce, 1954c].
Coniontis remnans Pierce, 1954c.
Coniontis lamentabilis Blaisdell [Pierce, 1954c].
Eleodes acuticaudus LeConte [Grinnell, 1908; Essig, 1931].
Eleodes gracilis distans Essig (not Blaisdell), 1931.
Eleodes omissus Essig (not LeConte), 1931.
Eleodes laticollis LeConte [Grinnell, 1908; Essig, 1931].
Eleodes grandicollis LeConte [Grinnell, 1908; Essig, 1931].
Eleodes elongatus Grinnell, 1908.
Eleodes osculans (LeConte) (= *Cratidus osculans*; see Doyen and Lawrence, 1979) [Essig, 1931].
Eleodes behri Grinnell, 1908 [Essig, 1931]. NEW SYNONYMY.
Eleodes intermedius Grinnell, 1908. NEW SYNONYMY.
Eleodes consobrinus Grinnell (not LeConte), 1908.
Eleodes omissus LeConte.
Nyctoporis carinata LeConte [Essig, 1931; Pierce, 1954a].

ZOPHERIDAE

- Noserus plicatus* LeConte [Pierce, 1954a; identified as *N. corrosus* Casey].
Phloeodes pustulosus LeConte [Pierce, 1954a].

These species are represented by reasonably complete remains, usually the pterothorax (including elytra) and abdomen, and may readily be associated with extant species. *Coniontis remnans* Pierce cannot be synonymized with any presently described species. It probably represents an unrecognized southern California species of the *opaca* group of Casey (1908). The paratypes of *C. pectoralis interrupta* were incorrectly assigned to *C. blissi* by Sphon (1973).

Coniontis puncticollis LeConte and *C. robusta* Horn, listed from La Brea by Grinnell (1908) are represented by remains which are too fragmentary to allow taxonomic assignment. Several other species attributed to the Rancho La Brea deposits clearly represent misdeterminations. For example,

Eleodes behri and *Eleodes intermedius* were described by Grinnell (1908) as new species of the subgenus *Blapylis*. Blaisdell (1909) suggested that both should be placed in synonymy under *E. parvicollis* Eschscholtz, which presently occurs in the area of San Francisco Bay. Cleaning of Grinnell's type specimens revealed that the elytral sculpturing is coarsely punctate, rather than tuberculate, as in *Blapylis*. The epipleuron is exceptionally broad, and slightly concave, as noted by Blaisdell, who attributed this to distortion caused by preservation. These specimens clearly represent *Eleodes osculans* (LeConte), but lack the characteristic long setation which was apparently lost during preservation. The abdomen of the type of *intermedius* still contained well preserved male genitalia, allowing further confirmation of its correct identity. The elytra identified by Grinnell as those of *Eleodes consobrinus* also represent *E. osculans*.

The specimens attributed by Essig (1931) to *Eleodes omissus* LeConte and *E. gracilis distans* Blaisdell are badly abraded remains of *E. acuticaudus* LeConte. In *acuticaudus* the elytral declivity bears a median longitudinal depression, and the mesocoxal cavities are separated from the metacoxal cavities by less than half the mesocoxal diameter. In *E. gracilis* the elytral declivity is slightly raised along the midline, and in *omissus* the declivity is flat. In both species the coxal cavities are more distant. *Eleodes omissus* is represented among undetermined Rancho La Brea material in the University of California Museum of Paleontology (Locality No. 2051). *Eleodes gracilis* is not presently known from the La Brea deposits, but has been identified from the Carpinteria deposit.

McKittrick Asphalt Deposit

The "classic" McKittrick asphalt deposit of vertebrate fossils is in Kern County, about one km south of McKittrick. Pierce's material came from adjacent sites (sites 3 and 4; LACMIP locality 260) along a road cut southeast of the vertebrate localities (Pierce, 1947b; Miller and Peck, 1979). Locality and age data are confused for Pierce's McKittrick specimens, which are probably younger than the vertebrate fossils (Miller and Peck, 1979). Unstudied *Eleodes* are present in material from the vertebrate fossil localities, and *Eleodes* has also been found in asphalt deposits near Maricopa in Kern County.

At present the only tenebrionid species recorded from the McKittrick deposits is *Parasida mckittricki* Pierce, 1954a. The holotype consists of the pterothorax, elytra and the abdominal sternites, with the right rear leg still articulated with the body. This specimen is remarkably preserved, clearly showing the original cuticular sculpturing, and by comparison with museum specimens is easily associated with the *costipennis* complex of *Stenomorpha*. The holotype of *Stenomorpha mckittricki* is clearly conspecific with

beetles which presently occur in the vicinity of McKittrick. The excellent preservation of the type specimens suggests that they may have become embedded in the asphalt very recently; certainly they are less modified than *Eleodes* fossils from the Maricopa or Rancho La Brea deposits. Because Pierce's description was restricted only to the posterior part of the body, *Stenomorpha mckittricki* is redescribed here.

Stenomorpha mckittricki (Pierce)

(Fig. 1)

Parasida mckittricki Pierce 1954a:43.

Body elongate, suboval, constricted at waist, convex; black with sparse covering of short, decumbent setae; legs reddish brown. Epistoma, frons and genae with closely set large punctures, separated by less than puncture diameter anteriorly, becoming sparser on vertex; large punctures irregularly interspersed with much smaller, sparse punctures; mentum transversely oval, shallowly and narrowly emarginate anteriorly, coarsely, closely punctate; antennae with 1st segment about twice as long as broad, 2nd segment subquadrate, 3rd segment about 4 times length of 2nd, segments 4–9 trapezoidal, about 1.5 times as long as broad, segments 9–10 about 1.5 times broader than long, segment 11 small, globular, amplexed in 10; eyes elongate oval, barely emarginate in front. Pronotum broadly, shallowly emarginate anteriorly, with acutely rounded anterior angles; lateral margins evenly arcuate, upturned; posterior margin evenly arcuate, with angles obtuse, reflexed; disk set with coarse, contiguous punctures, becoming coarser laterally and sharply punctatorugose near lateral margins; hypomera and sternum very coarsely, shallowly and sparsely punctate; prosternal process gradually declivous posteriorly, not projecting. Elytra finely, sparsely and shallowly punctate with raised medial margin and 4 prominent, sharply rounded longitudinal costae; costae anastomosing posteriorly, 1st (innermost) and 2nd usually fusing about $\frac{3}{4}$ posteriorly, 3rd terminating $\frac{3}{4}$ posteriorly, and 4th fusing with 1st and 2nd near elytral apex; 4th costa forming pseudoepipleuron, true epipleuron short, extending from 3rd to 5th abdominal sternites, not reaching elytral apex; abdominal sternites alutaceous to finely rugose or finely, asperately rugose. Femora punctatorugose to rugose; tibiae faintly rugose or very sparsely, finely tuberculate. Length, 11–16 mm; greatest elytral width, 5–7.5 mm.

Holotype, consisting of posterior half of body, from McKittrick Asphalt Deposit, Pierce Site 4, depth 4', Kern Co., California; Invertebrate Paleontology type no. 3064, Natural History Museum of Los Angeles County; 1 paratype, same data; 4 paratypes, same data but Pierce site 3.

Modern material examined.—130 individuals, California, Kern Co., 1.6 km (1 mi) NE McKittrick, March 19, 1975. J. Doyen.

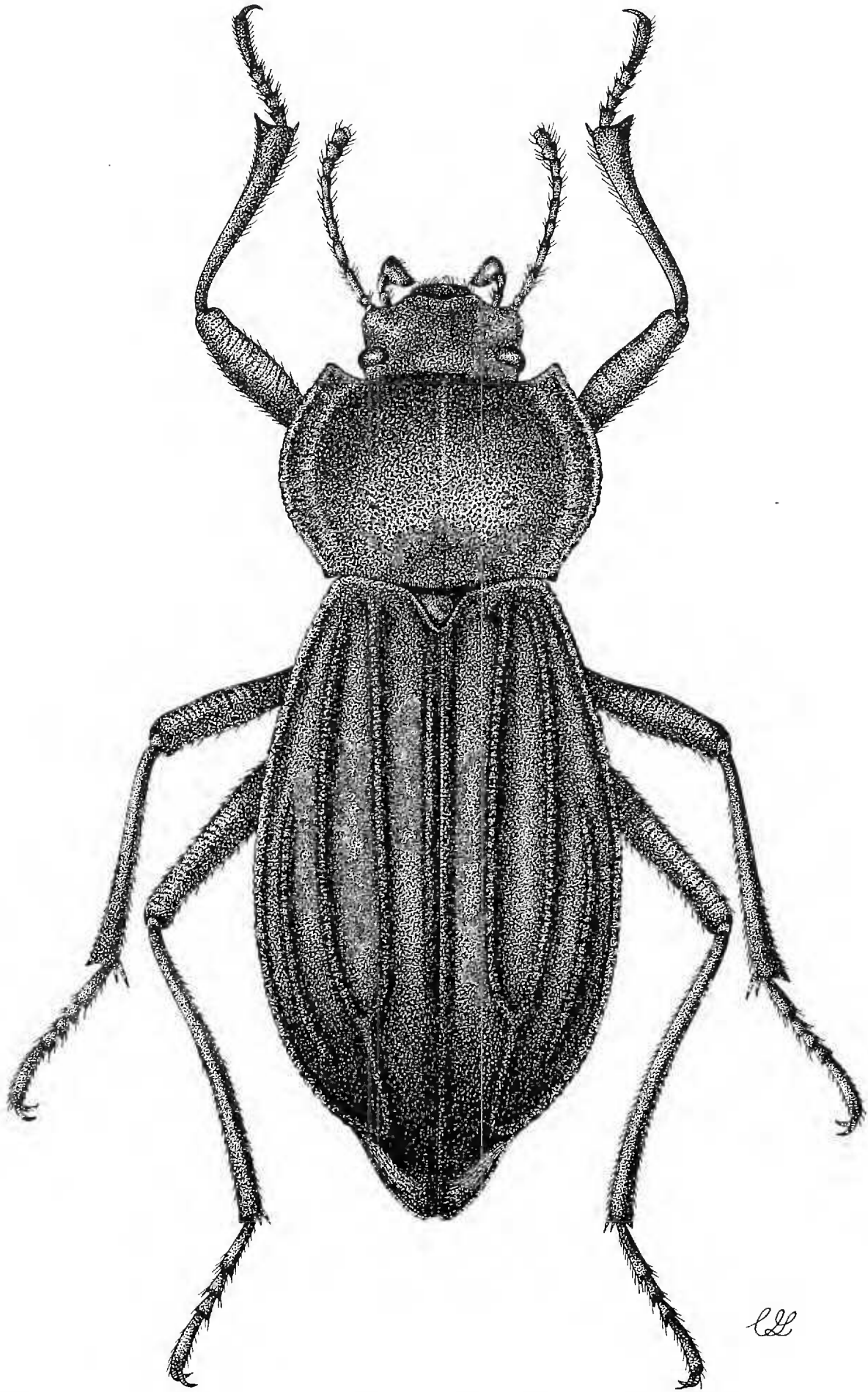


Fig. 1. Dorsal aspect of female of *Stenomorpha mckittricki* (Pierce).

Remarks.—*Stenomorpha mckittricki* is known only from the region immediately around McKittrick, where it occurs on the eroded badlands adjacent to the San Joaquin Valley. During its limited period of activity in early to mid-spring it can be exceedingly abundant.

Stenomorpha mckittricki is similar to *S. costipennis* (LeConte) and *S. neutralis* (Casey). Both of these species have black legs (red in *mckittricki*) and have the integument glabrous or with very short, sparse setae (longer, denser in *mckittricki*). *Stenomorpha costipennis* and *neutralis* occur north of the distribution of *mckittricki*, at various localities in Kern, Kings and Fresno Counties, along the western margin of the San Joaquin Valley.

Asphalt Deposits at Carpinteria

The Carpinteria asphalt deposit is located about 2 km southeast of Carpinteria, Santa Barbara County. Fossils were first discovered in the Carpinteria asphalt quarry in 1927, and excavations were initiated by the Santa Barbara Museum of Natural History. After the quarry was abandoned, the site was used as a refuse dump, beginning about 1940. Subsequently the natural topography of the area was so drastically altered by human activities that the asphalt beds are no longer accessible for study.

Tenebrionids are here recorded from Carpinteria for the first time. Specimens are deposited in the Santa Barbara Museum of Natural History and the Natural History Museum of Los Angeles County. A detailed treatment of the fossil insect fauna of Carpinteria is in preparation by Miller. Fragments of unidentified *Eleodes* occur in the Carpinteria deposits, as well as the species listed below.

Eleodes acuticaudus LeConte; 6 specimens, elytra and abdomens

Eleodes laticollis LeConte; 15 specimens, elytra and abdomens

Eleodes gracilis LeConte; 5 specimens, elytra and abdomens

Eleodes grandicollis Mannerheim; 1 prothorax

Eleodes giganteus Mannerheim; 2 prothoraces

Discussion and Summary

A total of 18 species (16 Tenebrionidae, 2 Zopheridae) can be definitely identified from the California asphalt deposits. The Rancho La Brea deposit, with 13 species of Tenebrionidae and 2 Zopheridae, comprises the richest fauna, but probably only because it has been more completely studied. The assemblage from Carpinteria, represented by only a small sample, contains 5 species, including 1 not yet confirmed in the Rancho La Brea material.

The 18 species represent a little over half of the cumulative number of species attributed to the asphalt deposits by various authors. Most of the reduction results from placing Pierce's taxa of *Coniontis* in synonymy. Sev-

eral species have been deleted from the Rancho La Brea list because of misidentification. In particular, the subgenus *Blapyllis* of *Eleodes* is not represented among material we examined.

With the possible exception of *Coniontis remnans* the fossils recovered from the asphalt deposits represent species which occur in the same regions today. The three most abundant species in the Rancho La Brea material, *Eleodes acuticaudus*, *E. osculans* and *Coniontis abdominalis*, are very common in remnants of coastal scrub and dry woodland habitats in southern California. *Coniontis lamentabilis* occurs in coastal scrub, generally on maritime bluffs or behind coastal sand dunes. The remaining species occur in many semiarid habitats in southern and central California, and *Noserus plicatus*, *Phloeodes pustulosus* and *Nyctoporis carinata* are most abundant in woodland situations, ranging into coniferous forest. It is significant that species which are restricted to woodland or forest habitats have not been recorded from the fossil deposits. For example, *Coelocnemis magna* LeConte, *C. californica* Mannerheim and *Cibdelis blaschkei* Mannerheim are extremely common in southern California woodland. These are distinctive species which would be easily recognized if present in the asphalt deposits.

Contrary to popular belief (i.e. Stock, 1956), the "pits" at Rancho La Brea do not represent deep pools of liquid asphalt which trapped unwary animals continuously for 40,000 years. Recent studies (Woodard and Marcus, 1973) and continuing excavation (W. A. Akersten, pers. comm.) have revealed a far more complex situation. Many insects, including tenebrionids, were probably trapped in relatively shallow puddles of asphalt, while others appear to have been deposited in stream sediments and preserved by subsequent asphalt impregnation of the sediments. Paleoecological interpretation of the tenebrionids recorded from Rancho La Brea is difficult due to uncertainties in age and mode of accumulation. Pierce's material is dominated by specimens from "Pit (?)" and "Bliss '29," which may include a large amount of Recent contamination. Pit A, also dominant in Pierce's material, was placed among the younger accumulations by Howard (1962), based on fossil bird faunal composition. Overall, the recorded tenebrionids suggest a drier and warmer period than implied by most Rancho La Brea fossils. This may reflect differences in age (the beetles being comparatively younger) or habitat (the beetles walking or being carried by water from adjacent drier habitats). The insects associated with Late Pleistocene vertebrate faunas are too few in number for useful comparison. Study of specimens from the recent excavation of Pit 91 may allow more meaningful comparisons, and could reveal a more diverse fauna.

The tenebrionid species represented by the Carpinteria fossils all presently occupy dry scrub and woodland habitats in southern and south central California. *Eleodes grandicollis* and *E. giganteus* range north to the San

Francisco Bay region, and *E. acuticaudus* to Monterey County, but in the northern portions of their ranges these species occupy areas of local aridity or with exceptionally well-drained soils. Thus, the tenebrionid assemblage indicates a climate and ecological situation similar to that now present at Carpinteria, rather than the predominantly moister environment suggested by vertebrate and plant fossils studied by Chaney and Mason (1933), DeMay (1941) and Wilson (1933).

The only tenebrionid species recorded from Pierce's McKittrick material is presently restricted to the McKittrick region. These specimens may be subfossil material which became embedded in the asphalt very recently, and are of very limited use in paleoecological reconstruction. The *Eleodes* from the "classic" vertebrate localities probably represent a different age, and may be more useful indicators of past environments at the McKittrick site.

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Footnote

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